Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*)

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Abstract: Density-dependent aggression, emigration, mortality, and individual growth have been identified in wild lotic salmonid populations. However, most work is limited to fish in the genus *Salmo*, and few studies consider density dependency coupled with observations of energy acquisition. We attempt to quantify density-dependent growth, size, and energy acquisition for a population of brook trout (*Salvelinus fontinalis*) in Appalachia, where the species is food-limited and population densities are low. Brook trout populations were intensely monitored over the course of 2 years at several sites within a watershed in eastern West Virginia. Tagging provided specific growth estimates, and diet analyses allowed for estimation of energy acquisition relative to maintenance requirements for adult fish. Young-of-the-year (YOY) brook trout exhibited density-dependent size relationships, but the intensity of density dependency varied substantially among months, with progressively decreasing slopes. Adult individual growth and excess energy acquisition was density-dependent, but only during periods when temperatures were warm and energy intake was low. The strong influence of temporal variability in density dependence of YOY size, as well as adult fish size, individual growth, and energy acquisition, suggests that density dependency in Appalachian brook trout may be driven by periodic prey resource scarcity.

Résumé : On a identifié de l'agression, de l'émigration, de la mortalité et de la croissance individuelle dépendantes de la densité chez des populations sauvages de salmonidés d'eau courante. Cependant, la plupart des recherches se sont concentrées sur des poissons du genre *Salmo* et peu d'études ont tenu compte de la densité-dépendance en fonction de l'acquisition de l'énergie. Nous tentons de mesurer la croissance, la taille et l'acquisition de l'énergie en fonction de la densité dans une population d'ombles de fontaine (*Salvelinus fontinalis*) dans la région des Appalaches où l'espèce est limitée par la nourriture et où les densités de population sont basses. Nous avons suivi de très près des populations d'ombles de fontaine pendant 2 années à plusieurs sites dans un bassin versant de l'est de la Virgine Occidentale. Le marquage a fourni des estimations spécifiques de la croissance et des analyses du régime alimentaire ont donné des estimations de l'acquisition de l'énergie en fonction des besoins du maintien chez les poissons adultes. Les jeunes de l'année (YOY) présentent des relations de dépendance de la densité pour la taille, mais l'intensité de la densité-dépendance varie considérablement d'un mois à un autre et les pentes diminuent progressivement. La croissance individuelle et l'acquisition d'énergie excédentaire chez les adultes sont dépendantes de la densité, mais seulement durant les périodes de température élevée et d'ingestion faible d'énergie. La forte influence de la variabilité temporelle de la densité-dépendance sur la taille des YOY et sur la taille, la croissance individuelle et l'acquisition de l'énergie des adultes laisse croire que la densité-dépendance chez les ombles de fontaine des Appalaches peut s'expliquer par une rareté périodique des ressources en proies.

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Introduction

Identifying density-dependent processes is a critical though often difficult step in assessing fish population dynamics. Density dependency occurs when intraspecific exploitation or interference competition increases with density, which can lead to elevated mortality rates, a greater propensity for individuals to emigrate, and (or) reduced growth rates (Rose et al. 2001). Such responses may be related to one another, as density-dependent individual growth may affect time spent susceptible to certain predators, thereby affecting mortality (Werner and Gilliam 1984). Despite the potentially important consequences, determining if density dependency is occurring can be difficult in wild populations. Strong temporal or spatial variability may mask density-dependent responses (Ray and Hastings 1996). Furthermore, density dependency may be temporally variable (Webster 2003), rendering sampling periodicity a critical factor.

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Density-dependent individual growth and size relationships in populations of lotic salmonids are commonly detected, though exceptions occur. Observational and experimental work has identified negative relationships between density and individual growth or size (regarded as a surrogate for growth), usually with fish in the genus *Salmo* (Vøllestad et al. 2002; Sundström et al. 2004; Vincenzi et al. 2007). The repeated occurrence of strong density-dependent individual growth and size relationships at low population densities has led to the suggestion that exploitative competition is the operating process, as space is unlikely limited at low densities (Jenkins et al. 1999; Post et al. 1999; Rincón and Lobón-Cerviá 2002). At high (≥ 2 individuals·m^{-2}) densities, however, space may become so limiting that decreasing individual growth occurs simultaneously with elevated mortality (Lobón-Cerviá 2007). Despite the growing body of evidence demonstrating density-dependent individual growth in lotic salmonids, studies reporting a lack of such relationships also exist (Rincón and Lobón-Cerviá 2002; Grant and Imre 2005).

Consideration of ontogeny may be crucial when assessing density dependency in lotic salmonids. Though some report that younger age classes exhibit greater density-dependent individual growth (Jenkins et al. 1999), several others have demonstrated the opposite scenario (Rincón and Lobón-Cerviá 2002; Arnekleiv et al. 2006; Einum et al. 2006). Energetic demand and territory size increase with increasing body size (Keeley and Grant 2001; Einum et al. 2006); therefore the idea that density-dependent individual growth increases as fish age is intuitive. However, the point at which density dependency begins to occur and the degree to which it is maintained in a cohort of lotic salmonids may be variable among populations, species, and environmental conditions.

Appalachian brook trout (*Salvelinus fontinalis*) represent a potentially informative case study to test the universality of density dependency in lotic salmonids. Glacial retreat since the Pleistocene confined most Appalachian brook trout populations to headwater watersheds, where streams are very low in productivity and often affected by acidic deposition. As a result, brook trout densities are typically low ($\ll 0.5$ N·m^{-2} in some cases) relative to salmonid densities observed elsewhere. The age and size structure of Appalachian brook trout populations are also relatively unique. Though young-of-the-year (YOY) emerge in the spring and grow rapidly during their first growing season, adults seldom live beyond 2 years and rarely grow longer than 200 mm (Whitworth and Strange 1983). Such environmental and life history attributes are atypical of previous studies addressing salmonid density dependency.

We sought to determine the degree to which individual growth, energetic gain, and body size exhibit density dependency in Appalachian brook trout. The current study complements previous investigations on seasonal dynamics of prey importance and energetic gain (Utz and Hartman 2006, 2007; Utz et al. 2007). Specific questions that were addressed include the following: (*i*) how does individual growth vary throughout the year between age classes, and with respect to energy acquisition, (*ii*) is density-dependent individual growth and size exhibited in populations of Appalachian brook trout and, if so, do such relationships vary with seasonal change, and (*iii*) do density-dependent individual growth and size dynamics differ between adults and YOY?

Materials and methods

Site and brook trout population description

All sites were located in the Middle Fork River watershed within the MeadWestvaco Ecosystem Research Forest in Randolph County, West Virginia, USA. Land use in the watershed (and riparian areas of each study reach) consists of secondary-growth hardwood forest. Nine first- and second-order sites were selected to encompass a range of stream sizes and brook trout densities (Table 1); all supported YOY throughout the study. The close proximity (≤ 6 km distance between sites) likely rendered variation in flow regimes among sites negligible. Because of nearly identical climatic and riparian canopy conditions, mean temperature differences were <2 °C. No species of salmonid other than brook trout were collected over the course of the study.

The brook trout population in the Middle Fork River is typical of those in the Appalachians. YOY exhibit rapid growth rates during their first growing season, but growth slows thereafter; the mean size of individuals not deemed in the YOY cohort was 123.8 ± 1.2 mm (only 33 out of 3166 collected exceeded 200 mm in length). Although YOY are easily distinguishable from age-1+ fish using length–frequency histograms, delineation of adults to specific cohorts is impossible without use of scales or otoliths (not collected in the current study). In a separate study, age delineation using scales and otoliths within the Middle Fork River watershed suggested that 91% of age-1+ individuals consisted of 1- and 2-year-old trout; the remainder were age-3 (Stolarski 2007). All fish not considered YOY are hereafter referred to as adults.

Fish and habitat sampling

Fish were sampled 11 times in 2004 and 2005 (March, May, June, and July during both years and August, September, and December during 2004). The study design focused on consumption dynamics; thus warm seasons were overrepresented. At each site, a 200 m reach of stream was blocked with nets and triple-pass electrofished using DC current backpack units. All fish were immobilized with a dilute solution of clove oil and stream water; the fork length and weight of each fish were recorded. Ten fish representing the range of adult sizes at each site were subjected to gastric lavage for diet analysis during each sampling event. Adult fish were tagged with a unique identifier code in the caudal fin using visual implant elastomer tags (Northwest Marine Technology, Shaw Island, Washington) in May 2004 and 2005 (additional tagging was not performed because of the long handling time required). Habitat sampling was conducted during baseflow conditions in August 2005 and included measurements of wetted width (used to calculate fish density).

Consumption and maintenance ration

We estimated instantaneous energy available for growth as the difference between energy consumed and mainte-

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Table 1. Study site attributes, Middle Fork River watershed, West Virginia.

Site	Strahler order	Basin area (km^2)	Mean riffle depth (cm)	Mean pool depth (cm)	Mean trout density ($N \cdot m^{-2}$)
Brush	1	0.83	7.58	19.30	0.115
Kittle, low	2	15.38	13.00	23.78	0.035
Kittle, mid	2	5.26	11.94	20.67	0.085
Kittle, up	1	2.05	7.46	17.54	0.237
Light	2	5.24	9.92	19.62	0.053
Mitchell	1	1.78	7.87	15.53	0.186
Rocky, low	2	9.94	15.21	30.83	0.028
Rocky, up	2	6.44	11.22	32.52	0.046
Sugar	1	1.64	8.09	27.92	0.151

Note: "Low", "mid", and "up" refer to the location of different sites on the same stream separated by ≥2 km.

nance ration for each fish and time interval. Estimated maintenance ration (EMR, in joules per gram of fish wet weight per day) was the consumption necessary to achieve zero growth in mass over 1 day. The EMRs were calculated based on a revised and validated bioenergetics model for brook trout (Hartman and Cox 2008) using fish weight, fish energy density, and water temperature as variables. Brook trout energy densities were calculated from mean energy density in collected fish using a Salmonidae dry weight – energy equation (Hartman and Brandt 1995). Consumption estimates were calculated based on the model proposed by Eggers (1977). Individual prey were converted to units of energy using taxon- and stage-specific dry weight – energy equations from Cummins and Wuycheck (1971), and the total energy in each gut were summed for each fish.

Daily consumption for each fish was calculated using the Eggers model, gut energy content, and temperature-specific gastric evacuation rates. The model is of the form

$$C = (\text{GEC} \cdot R)/W$$

where C is hourly consumption rate ($J \cdot g^{-1} \cdot h^{-1}$), GEC is gut energy content, R is the gut evacuation rate, and W is the weight of the fish. The hourly consumption rate is multiplied by 24 to convert consumption to a daily rate ($J \cdot g^{-1} \cdot day^{-1}$). Daily consumption estimates commonly use information on feeding intensity over a diel cycle. However, with knowledge of the diel feeding periodicity, or if there are no diel trends, single estimates of gut contents have been used successfully to estimate consumption in fish (Ruggerone 1989; Whitledge and Hayward 2000). We assumed that because several studies found no diel trends in feeding of brook trout (Forrester et al. 1994; Sweka 2003; Mookerji et al. 2004), daytime collections of gut contents were adequate to describe consumption rates and any errors would be systematic across sites, seasons, and densities.

The Eggers model requires an estimate of gastric evacuation rate (GER) to estimate consumption. Earlier estimates of consumption (Utz and Hartman 2006) used GERs published for brook trout by Sweka et al. (2004). GERs in fish are known to be influenced by fat and energy content of prey (Elliott 1972; Jobling 1987; Jensen and Berg 1993), prey size (He and Wurtsbaugh 1993), and meal size (Jobling et al. 1977), which is influenced by pre-experiment fasting periods (Bull and Metcalfe 1997). Methods used to estimate GERs by Sweka et al. (2004) may have been biased by long

(5 days) pre-experiment fasting periods, as well as the use of fat, high-energy prey. To evaluate this, we compared the GER of Sweka et al. (2004) with other published salmonid exponential GERs (Fig. 1). We determined that other insect-feeding salmonids with shorter pre-experiment fasting periods had evacuation rates 3–8 times higher at a given temperature (Arctic char, *Salvelinus alpinus* (Amundsen and Klemetsen 1988); coho salmon, *Oncorhynchus kisutch* (Brodeur and Pearcy 1987); brown trout, *Salmo trutta* (Elliott 1972); rainbow trout, *Oncorhynchus mykiss* (Hayward and Weiland 1998); Chinook salmon, *Oncorhynchus tshawytscha* (Principe et al. 2007)) than those reported for brook trout. In addition to Sweka et al. (2004), Boisclair and Sirois (1993) published GER for brook trout feeding on *Artemia* that also showed slower GER than other salmonids. A study of the closely related Arctic char (Amundsen and Klemetsen 1988) found GER to fall in line with that of other salmonids feeding on natural insect or crustacean prey. Because food type, fat content, and fasting periods are such important influences on GER, we used previously published studies to develop a generalized salmonid GER model to predict evacuation rate of insect prey from temperature (analysis of variance, ANOVA, df = 14, $F = 38.53$, $p < 0.001$, $r^2 = 0.76$) and used this for calculating consumption of brook trout in this study (Fig. 1). The derived equation was

$$R = 0.0354 \cdot e^{0.119T}$$

where R is the gastric evacuation rate (h^{-1}) and T is temperature (°C).

Statistical analyses

Population estimates of all fish were calculated for each stream using the Zippin model in program CAPTURE (White et al. 1982) to estimate fish density. If fewer than 30 fish were captured, then the actual number of fish caught was substituted for an estimate (Riley and Fausch 1992). Fish in the YOY cohort were easily identified using length–frequency histograms for collections from May through December. Although some YOY were collected as early as May, they did not fully recruit to the electrofishing gear (i.e., YOY counts were stable rather than increasing at each site) until July. Therefore potential density dependency of mean size in the YOY cohort was analyzed from July through December 2004 only.

Fish density per site was calculated as the population esti-

Fig. 1. Comparison of exponential gastric evacuation rates (GER) for salmonids from various studies. Solid and shaded symbols represent those studies used to derive the equation shown, which was applied to estimate consumption in the current study.
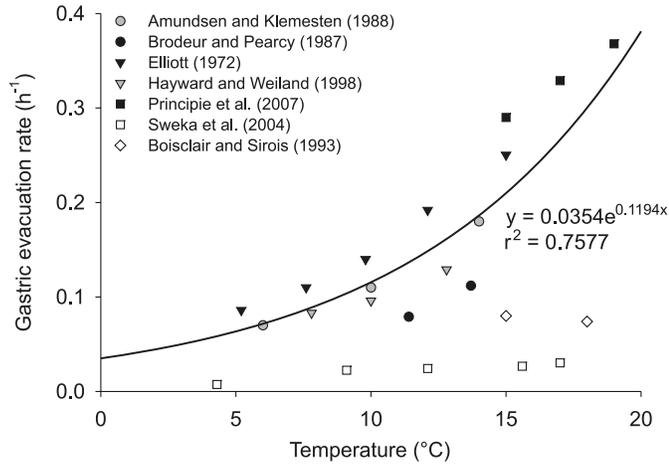
mate divided by the wetted area (m²) during base flow. Early analyses considered the size-adjusted variable effective density (Σ(fish length)² divided by wetted area; Post et al. 1999) and YOY density as alternative predictor variables to the density of all trout. However, for our analyses, we considered only density for several reasons. Density was strongly correlated to both effective (Pearson's correlation coefficient = 0.96, $n = 9$, $p < 0.0001$; site-specific averages across all sampling events) and YOY density (Pearson's correlation coefficient = 0.96, $n = 9$, $p < 0.0001$; site-specific averages during sampling events when YOY were collected). Further, density consistently proved to be a superior predictor of response variables and represented the most parsimonious independent predictor among the density measures.

The size variable used in growth and size analyses was fork length due to the poor accuracy of weight estimates for small fish and the confounding effects of egg hydration on the weights of spawning females during fall. Growth (applied to recaptured fish) was calculated from the following equation (from Elliott 1975):

$$G_w = \ln(L_t/L_0)/\Delta t \times 100$$

where G_w is instantaneous growth (percentage of initial length gained between times 0 and t), L_t is the length at time t, L_0 is the initial length, and Δt is the amount of time elapsed between capture events (in days).

To assess density-dependent size relationships, a repeated-measures analysis of covariance (ANCOVA) was run on site-specific mean fish length for adults and YOY separately. We assumed that size would be temporally autocorrelated, as a proportion of the individuals collected would be recaptures but that the degree of autocorrelation would decay with time as fish either dispersed or grew. We therefore selected an autoregressive covariance structure. Initial model parameters included density, month, a month $\times$ density interaction term, and basin area. If basin area was not significantly related to mean fish size, it was removed and the models were reassessed. We considered both linear and power relationships between fish size and density. The model with the lowest AIC (Akaike's information criterion)

value was selected. Following the model selection, mean fish size was regressed with mean density across all months (if the month $\times$ density term was not significant) or each month separately (if the month $\times$ density term was significant) to estimate the variation in mean size explained by density.

Potential density-dependent relationships in mean observed growth and mean excess energy acquisition were also explored. Each month was classified based on feeding success (from Utz and Hartman 2006) and temperature. Months fell into one of three seasons that were analyzed separately: favorable feeding conditions (May–June; four sampling events), poor feeding – warm (July–September; four sampling events), or poor feeding – cold (December–March; three sampling events). We were less concerned with temporal autocorrelation of variables for these analyses as we assumed that growth and energy acquisition were subject more to food availability than to resident fish characteristics. Therefore, for both individual growth rates and excess energy, the site-specific means were treated as response variables and site-specific mean density and basin area were treated as independent variables. To explore how trout density affected growth and excess energy acquisition, a multiple regression model was constructed with basin area and density as initial predictor variables. Basin area was removed if it proved to be unrelated to the dependent variable. Model AIC values were used to select linear versus power fits. All statistical procedures were performed in SAS (version 9.1, SAS Institute Inc. 2003).

Results

Variation in the growth rates of tagged fish reflected trends in excess energy acquisition (Fig. 2). Brook trout consumed the most excess energy and exhibited the largest individual growth rates during spring and early summer. Once energetic intake dropped in midsummer, growth fell to near zero and remained at low levels until the following spring. Trends in both growth and excess energy acquisition appeared to be consistent between 2004 and 2005, though the period of greatest excess energy intake (May 2004) did not directly correspond to the greatest observed growth rates. The most substantial deviance between the two variables occurred when the second greatest excess energy intake recorded (May 2005) did not correspond to the highest individual growth rates; this may have been an artifact of the poor recapture rate (13 fish). Unfortunately, fish tagging did not occur until May 2004; thus individual growth rates between March and May 2004 were not available.

Although mean fish length in the YOY age class was significantly related to trout density, temporal variation in the strength of density dependence was observed. Because month ($F = 123.5$, $p < 0.0001$), density ($F = 53.0$, $p < 0.0001$), and the density $\times$ month interaction term ($F = 14.1$, $p < 0.0001$) were significant in the selected model, mean length was regressed with density separately from July through December 2004. Density dependency in mean YOY size increased as the year progressed, with the most negative slope observed in December (Fig. 3). A linear relationship was superior to a power curve, whereas basin area was not significant. The repeated-measures approach proved

Fig. 2. Adult brook trout (*Salvelinus fontinalis*) mean growth rate (±95% confidence intervals; solid circles) and mean excess energy acquisition (estimated daily consumption – estimated maintenance ration; shaded bars) averaged across all sites. Month represents the ending month of the growth estimates. Numbers above error bars represent the sample size of recaptured tagged fish; each bar represents a sample size of 90 consumption estimates. March and May 2004 sampling events are not shown as fish were initially tagged in May 2004.
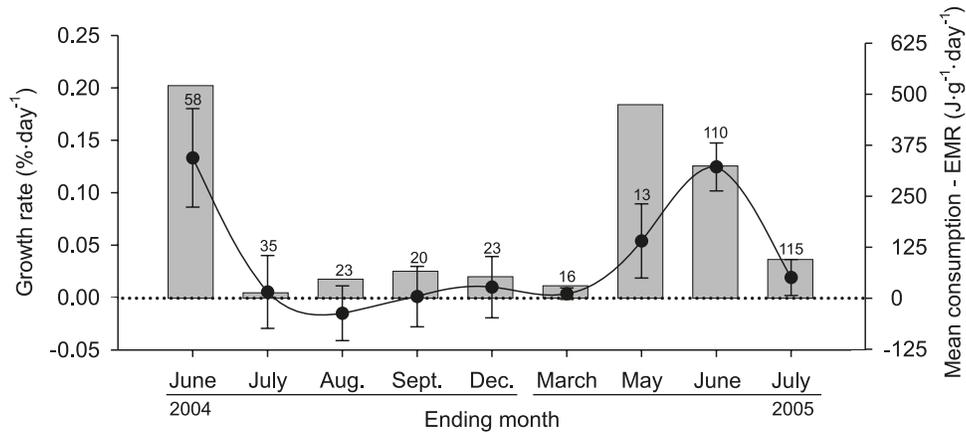

Fig. 3. Mean site-specific young-of-the-year (YOY) length as a function of trout density and sampling month (2004 only); β represents the slope of the linear relationship.

Fig. 4. Mean site-specific adult fish length as a function of mean trout density across all sampling events. Error bars represent 95% confidence intervals; numbers above or below the error bars represent site-specific sample sizes.
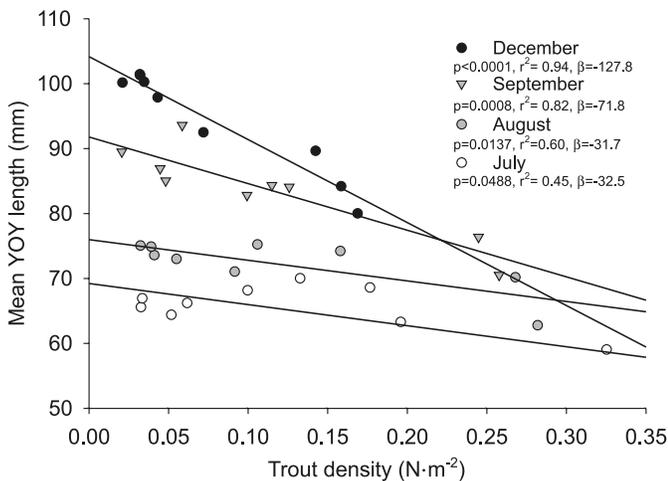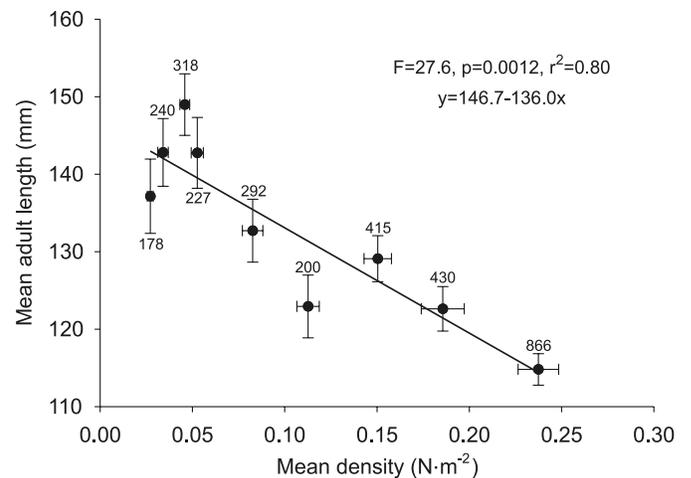

appropriate: the null model likelihood ratio test was significant at the level of $\alpha = 0.05$ ($\chi^2 = 9.08$, $p = 0.0026$)

Density dependency of mean length in the adult age class was also observed but appeared to be consistent through time. In the selected ANCOVA model, month ($F = 5.7$, $p < 0.0001$) and density ($F = 44.6$, $p < 0.0001$) were significant, whereas the interaction term was not ($F = 1.24$, $p = 0.2863$). As in the YOY cohort, a linear fit with density was found to be superior. When mean adult length was regressed with mean density across all sampling periods, a significant negative linear relationship was evident (Fig. 4).

Mean excess energy acquisition was related to trout density, but only during the period of poor feeding and warm temperatures (July–September; Fig. 5a). During this season, a linear fit with density proved to be the best model and explained much of the variability in mean energy acquisition. In the remaining two seasons, however, no relationships with density were significant.

Patterns of density dependency in tagged fish growth reflected trends in excess energy acquisition. The only signifi-

cant relationship was observed during the period of warm temperatures and poor feeding (Fig. 5b). Here, a power relationship proved to be the best model and explained approximately half the variation in mean growth. No significant relationships between mean trout density and mean growth were observed in the other seasons. Only six streams were regressed during the poor feeding – cold season because of poor recapture rates and absence of tagged fish in March 2004.

Discussion

Density-dependent growth and size relationships in Middle Fork River brook trout do exist but appear to be driven by energetic dynamics during metabolically stressful periods. From July through September, mean energy acquisition bordered on maintenance rations; fish in low-density streams fed above maintenance ration, whereas fish residing in high-density streams fed below. Consequences of density-dependent feeding were reflected in mean summer–fall in-

Fig. 5. (*a*) Mean site-specific excess energy acquisition (estimated daily consumption minus estimated maintenance ration) and (*b*) mean growth as functions of brook trout density. Three seasons were separately analyzed: spring ("Favorable feeding"; May–June), when temperatures were warm and consumption was high; summer ("Poor feeding – warm"; July–September), during high temperatures and consumption; and winter ("Poor feeding – cold"; December–March), when temperatures were cold and consumption was low. Solid lines denote significant relationships; error bars represent 95% confidence intervals. Site-specific sample sizes are provided in the lower right corner for excess energy acquisition and adjacent to each point for growth.
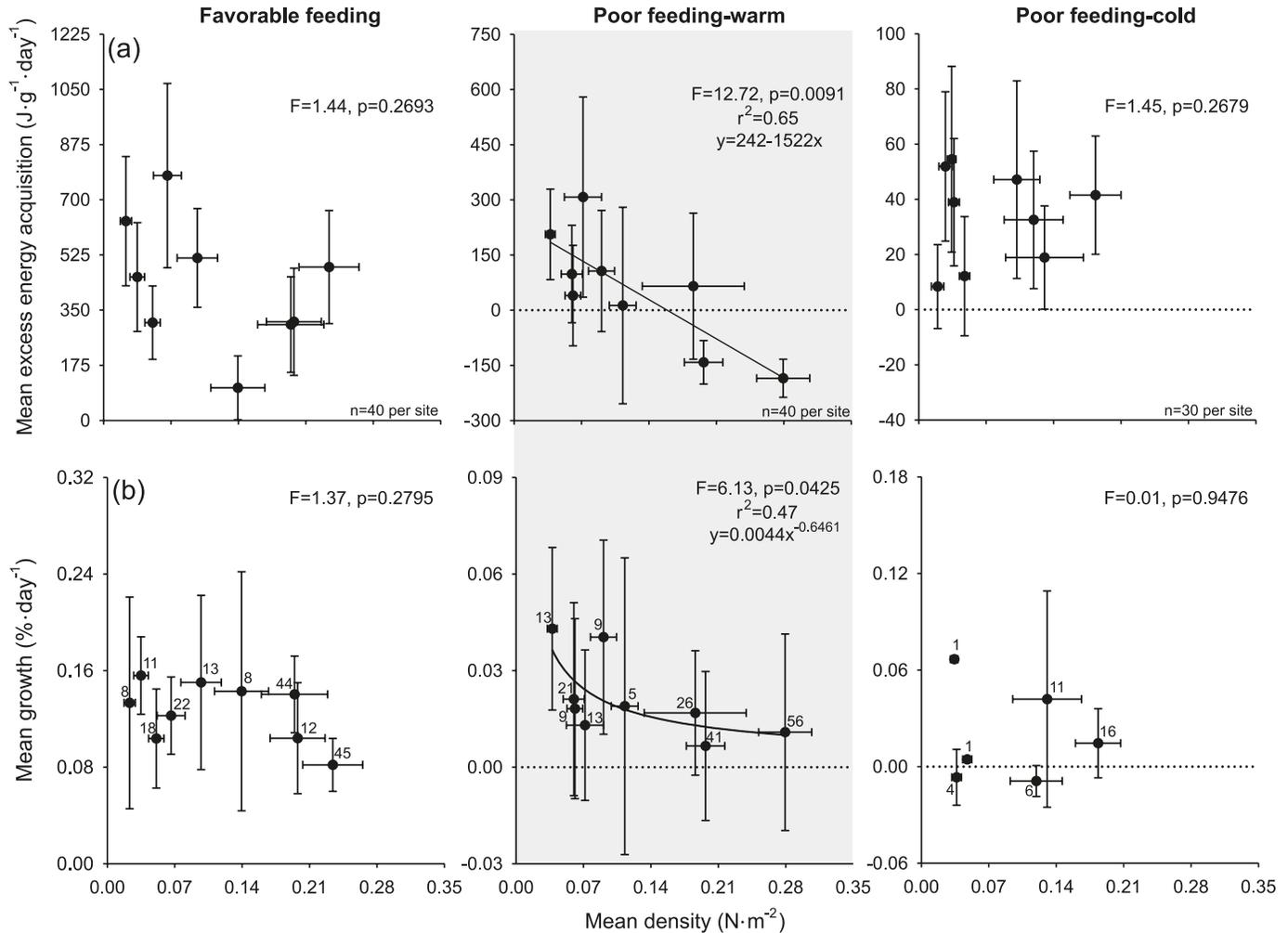
dividual growth, which likely led to the overall trends observed in density-dependent mean size between streams. High energy intake (assumed to be directly related to prey availability; Utz and Hartman 2006) appears to buffer density dependency during spring, whereas cold temperatures and reduced metabolic demand may render density dependency in winter months less significant during this period (though the small sample size of recaptures during winter likely disallows strong inferences on growth).

The observed trends in density-dependent individual growth of tagged adult fish are somewhat surprising in light of the size structure among sites. Both mean adult fish size and mean individual growth rates for recaptured fish were negatively related to density during the summer months. Larger fish, however, should be expected to naturally exhibit slower growth rates in terms of the proportion of initial length added over time because growth capacity declines with increasing size (Jobling 1983; Bjornsson and Tryggvadottir 1996). Results showing density-dependent individual

growth in adult fish despite the disparity in mean size among sites imply that density was a strong driver of individual growth rates. The concordance between feeding intensity and growth estimates, however, offers a mechanistic explanation of the observed trends (prey scarcity as reflected by energy intake).

That density dependency may be driven by periodic prey resource scarcity may lend a partial explanation as to why reports of density dependency vary. Though significant density-dependent size and individual growth relationships appear to be increasingly consistent in the literature, exceptions are noted (Rincón and Lobón-Cerviá 2002; Grant and Imre 2005). Seasonal trends in energy acquisition demonstrated in the Middle Fork River (Utz and Hartman 2006) seem to be consistent for brook trout in the eastern United States (Ensign et al. 1990; Carlson et al. 2007). Substantial fluctuations in energy intake due to variable prey availability have been observed in populations of lotic salmonids elsewhere (Kawaguchi and Nakano 2001; Rundio and Lind-

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ley 2008). Considering that most research addressing density dependency in lotic salmonids sample fish once within a year, previously reported results may have been partially affected by intra-annual variability in prey resources. Findings from this study warrant careful consideration of temporal variability in critical environmental factors (such as prey availability) when assessing density dependency.

YOY density-dependent size relationships also differed substantially among seasons. The weakest relationship between YOY size and density was observed in July, perhaps due to low absolute metabolic demand. However, as the year progressed and YOY fish grew, density dependency in mean size became stronger with time in both the slope of the relationship and the proportion of variance explained. The steepest slope appeared in December, after the period of time that most substantially affected the adult fish (summer–fall) had elapsed. Although others have shown increasing density-dependent consequences as fish age (Elliott and Hurley 1998; Rincón and Lobón-Cerviá 2002; Arnekleiv et al. 2006), the current analysis seems to be the first observational study to show such trends within a single growing season. In fact, the Middle Fork brook trout contrast trends demonstrated by Rincón and Lobón-Cerviá (2002) and Arnekleiv et al. (2006) in that density-dependent sizes were not observed for YOY cohorts in those systems. In a related manipulative experiment, Einum et al. (2006) report near identical findings to ours in populations of Atlantic salmon (*Salmo salar*) (compare our Fig. 3 with their fig. 1). Such trends have implications for other studies in which YOY density-dependent dynamics are examined: the choice of sampling period within the year may affect results.

Exploitation competition is the most commonly suggested driver behind density-dependent trends in lotic salmonids; our research lends cautious support to this notion. Prey resources, as suggested by excess energy acquisition, fluctuated substantially throughout the study. In the Middle Fork River watershed, density dependency in growth appeared in tagged fish only when prey resources were apparently low and temperatures were high, though our ability to make inferences during winter is limited due to poor recapture rates. Still, our findings suggest that exploitation competition is driving density dependency, which is often the conclusion drawn in related studies that did not quantify consumption or prey availability (Rincón and Lobón-Cerviá 2002; Imre et al. 2005; Arnekleiv et al. 2006). Yet exploitation and interference competition may not be mutually exclusive (Ward et al. 2007). Related studies (Rincón and Lobón-Cerviá 2002; Imre et al. 2005; Arnekleiv et al. 2006) suggest that fish densities similar to those observed in the Middle Fork River are too low to lend support for interference competition. This would seem a premature statement for the Middle Fork River population, as even in these low-density streams, ≥10 fish were retrieved from a single pool in some instances (R. Utz, personal observation). Therefore, interference competition should not be ruled out without concurrent examination of animal behavior in a given system.

Our findings contrast the few earlier examinations of density dependency in brook trout and may have management implications for the species. Previous studies in brook trout demonstrate either no density dependency in mean size (Hunt 1974, assessed in Imre et al. 2005; Dunham and Vin-

yard 1997) or weak density-dependent size relationships at much higher densities than those in the Middle Fork River watershed (Grant and Kramer 1990). High-density streams may be important source reaches for brook trout populations at the watershed scale (Petty et al. 2005). However, density-dependent growth in these systems, coupled with greater energy intake in lower reaches, suggests that low-density reaches are important for feeding and growth. Density dependency in YOY individual growth may also be critical for population regulation, as energy intake is strongly dependent on seasonally variable inputs of large terrestrial prey (Utz and Hartman 2007; Utz et al. 2007) only available to fish with a large enough gape.

Acknowledgements

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